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The sensillae and related structures on the gills of nymphs of the genus *Caenis* (Ephemeroptera). By L. E. S. EASTHAM, M.A., M.Sc.
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THE SENSILLAE AND RELATED STRUCTURES ON THE GILLS OF NYMPHS OF THE GENUS *CAENIS* (EPHEMEROPTERA)

By L. E. S. Eastham, M.A., M.Sc.

[Read 4th March, 1936.]

With One Plate and Eight Text-figures.

Contents.

	PAGE
Introduction	401
Methods	401
The distribution of sensillae on the gills	402
The campaniform sensillae	405
The trichoid sensillae	408
Sensillae on the gill-bearing segments	409
Sensillae in relation to habits	410
The sensillae in *C. horaria*	412
Summary	413
Literature	413

Introduction.

It was recently shown, Eastham 1932 and 1934, that the nymph of the Mayfly *Caenis horaria* L. exhibited peculiarities of gill oscillation involving (*a*) a transverse flow of water across the body and (*b*) the power to reverse that flow apparently at will. In the prosecution of that work it was discovered that the gills of this species and of others of the same genus were provided with a rich supply of sensillae on their surfaces.

No reference appears to have yet been made to such gill sensillae, and for this reason the following description seems apposite. Further, since the gills behave in the manner described and since that behaviour particularly in the matter of reversal appears to depend on the animal's ability to detect differences in the nature of its surroundings, a study of these sense organs might afford a basis for subsequent work on the environmental relations of the animals.

In the progress of the above-cited work it was found, as was to be expected, that *C. macrura* Steph., a larger form, behaved similarly to *C. horaria*. Because of the greater size, the larger number of sensillae on its gills and the greater size of those sensillae, *C. macrura* was chosen as the subject for study. A comparison of the two forms mentioned would suggest that gill sensillae might afford a valuable criterion in systematics.

Methods.

For the determination of numbers and distribution of sensillae on the gills, mounts in glycerine either of fresh or of preserved material were employed. In those cases where pigment in the underlying hypodermis obscured the view, the gills were treated with cold potash followed by carbol fuchsin. For sectioning the following fixatives were used, alcoholic bouin at 70° C., Carnoy's fixative

and corrosive sublimate. The first of these gave the best results. The sections were stained variously in Heidenhain's haematoxylin, methyl blue eosin and Mallory's triple stain, using iron alum as a mordaunt. Heidenhain's stain gave the best results for the cellular structures, while Mallory's stain gave the best differentiation for the chitinous elements, the results of which were readily confirmed by the former stain. Sections were cut at thicknesses from 5 to 8 μ and the preparations obtained with paraffin embedding were further checked with others which had been prepared after being double embedded in clove oil collodion and wax. Wax with a melting point of 54° C. was used. The nymphs employed were carefully compared with the exuviae left on the emergence of adults, which latter were kindly identified by Dr. K. G. Blair. In certain cases the gills of the skins of mature nymphs were fixed immediately on the emergence of the adults. Such gills are of course complete structures and represent the fullest development that these organs can attain. It was not possible to establish in all cases whether a nymph was in the ultimate or penultimate instar, and to this may be due the range in variation in the numbers of sensillae recorded in *Caenis macrura*.

The distribution of sensillae on the gills.

To avoid a lengthy description of the gross anatomy of the gills of *Caenis* reference may be made to Rousseau 1921 and Eastham 1934. There are six pairs, borne on the first six abdominal segments. Of these the first pair are reduced to slender immobile finger-like processes with normal trichoid sensillae projecting from their sides and tips. The second pair, the pseudo-elytra, act as protective gill covers to the remaining four pairs. Each of the latter consists of a semicircular plate fringed with branching filaments. These are the oscillating gills and in the ensuing description will be numbered from 1 to 4.

The pseudo-elytra.

Each pseudo-elytron is sub-quadrangular in shape with its anterior border approximately straight, the other borders being curved (fig. 1). It is slightly convex above and concave below with the exception of a triangular flat area along the median side, by means of which area the one pseudo-elytron fits over the other in the middle line of the body when the gills are not in motion. The curved border is fringed with long trichoid sensillae whose projection outwards and backwards is in alignment with the surface curvature of the organ. There are also a few such sensillae on the dorsal surface along the edge of the flat triangular area where it joins the rest of the pseudo-elytron. On the dorsal surface there are also a few plumose setae, short trichoid sensillae, the free ends of which are splayed out into a fringe. A covering of the dorsal surface by short fixed non-sensory spines may also be mentioned.

Central and peripheral areas on the under surface are distinguished by the presence and absence of campaniform sensillae respectively. One part of this peripheral area coincides with the above-mentioned triangular area. The lateral and posterior parts of the peripheral area are traversed by a band of fringed microtrichia which, starting at a point near to the place of attachment, passes more or less parallel to the gill's curved border ending near the postero-median angle of the organ. This band is composed of about ninety short rows of microtrichia, each row running transversely across the band (fig. 1). Each microtrichium is a prominent chitinous excrescence directed towards the nearest point of the pseudo-elytral border. As seen in surface view each

has a palmate appearance due to its free edge being produced into some eleven or twelve fine diverging points (fig. 2). The members in each row overlie one another as do tiles on a roof (fig. 3). That there is no sensory element

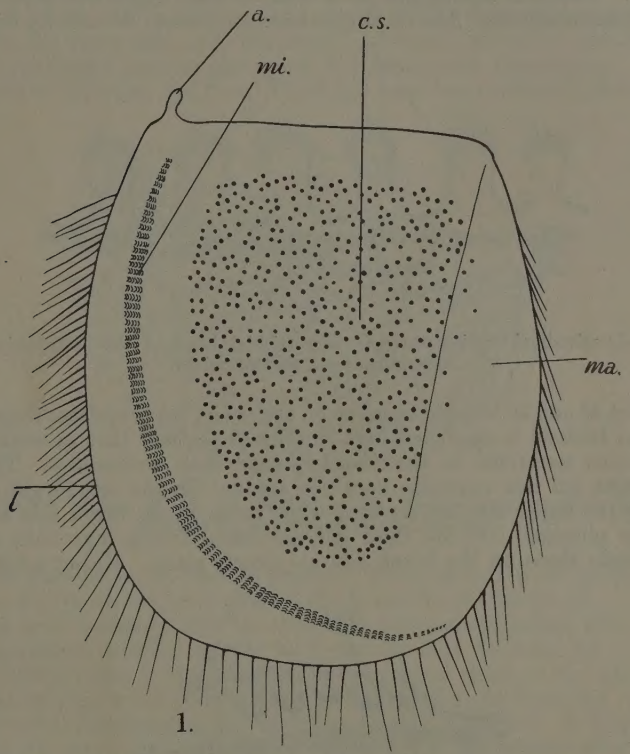

FIG. 1.—Lower surface of pseudo-elytron of *C. macrura*. *a*, articulation process; *mi*, microtrichial band; *c.s*, campaniform sensillae; *l*, lateral border; *ma*, median area.

in these structures is shown in these figures. The density and distribution of the campaniform sensillae in the central area of the under surface of the pseudo-elytron is shown in fig. 1.

The oscillating gills.

Mounts of any of the remaining gills (preserved material in spirit, or better, fresh material in glycerine) disclose a large number of sensillae on both gill surfaces.

The upper surface of each gill is divided into anterior and posterior areas by trichoid sensillae arranged in a band passing from the gill stalk to the opposite border (pl. 1, B1–B4). These sensillae are arranged in three roughly alternating rows, and each is deflected sharply from its point of articulation towards the posterior border of the gill so as to lie almost parallel with the gill surface. On the dorsal side of each of the first gills there are about 70 such setae.

The lower surface of each gill is similarly divided into anterior and posterior

areas by a band of trichoid sensillae. The latter band lies nearer to the anterior gill border than does the band on the upper surface and comprises about 60 elements (fig. 4). The remaining gills being successively smaller carry fewer sensillae. Thus the second gills have each on their upper side about 60 and on the lower about 55. The third gills have each about 55 and 40, the fourth

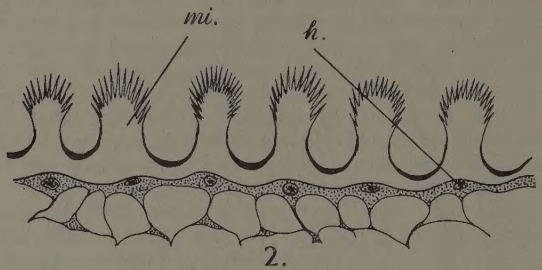

Fig. 2.—Longitudinal section through microtrichial band of the pseudo-elytron. *h*, hypodermis; *mi*, microtrichium.

gills about 48 and 30 trichoid sensillae on upper and lower surfaces respectively. The term trichoid is employed here in spite of the fact that in certain cases they possess serrations on their borders near their extremities. Typically, on the first gill this condition does not apply. On the second gill some of those on the upper side are serrated while those on the lower side are often distinctly plumose. On the third gill the dorsal trichia may have serrated edges, while those on the lower side are mostly plain. All but a few of the

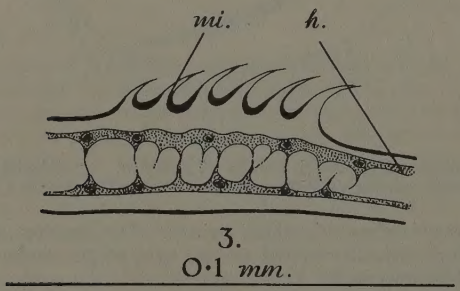

Fig. 3.—Transverse section through the microtrichial band of the pseudo-elytron. *h*, hypodermis, both upper and lower layers are shown; *mi*, microtrichium.

trichia on the fourth gill are plain with no sign of the serrations along their sides.

In addition to the trichoid sensillae the gills carry on both their surfaces many of the campaniform variety the distribution of which can be best described with reference to the positions occupied by the trichoid bands. On each upper surface, campaniform sensillae lie both anterior and posterior to the trichoid band. There are, except in rare instances, however, no sensillae of this kind anterior to the trichoid band on the lower surface (fig. 4). Further, with the exception of the first gill, there are fewer campaniform

sensillae on the upper than on the lower surface of each gill. As with the trichoid sensillae the numbers of the campaniform type decrease from before backwards on the gills. Considerable variation in the numbers of sensillae on the four pairs of gills in different individuals has been observed. Thus on the first gill from 110 to 140 have been found on the upper side and from 180 to 200 on the lower side. On the second gill from 125 to 220 and from 100 to 170 have been found on the upper and lower sides respectively. On the upper side of the third gill from 100 to 220 have been counted, while on the

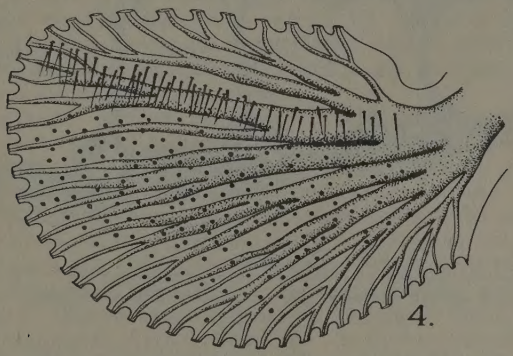

FIG. 4.—Lower surface of the 1st oscillating gill. Campaniform sensillae are shown posterior to the band of trichoid sensillae.

lower side from 50 to 150 may be present. From 45 to 115 on the upper side and from 0 to 60 on the lower side are the figures for the fourth gill.

When seen in surface view on treatment with carbol fuchsin after potash, the campaniform sensilla appears as a circular area bounded by a ring-like ridge of chitin which is continuous with the general chitin of the gill surface. This circular area is the terminal cap of the sensilla, the bounding rim being the edge of a chitinous cup in which the sensilla is lodged. A deeper focus indicates the gradually narrowing sensillary cup at the bottom of which is a small pore through which the sensilla nerve passes.

The campaniform sensillae.

Vertical sections through the organ show the proportions of the cup with reference to the terminal cap (figs. 5 and 6). The latter is slightly convex on its outer surface and appears to be attached at its edges to the overhanging rim of the gill epicuticula. That it is attached is suggested by the retention of the terminal cap in position after treatment with hot potash. The terminal cap best exhibits its detailed structure after double embedding in clove oil collodion and wax followed by Mallory's triple stain. It is then seen that the epicuticula forms the chitinous cup in which the organ rests. The terminal cap is differentiated into an outer layer similar to the normal epicuticula but thinner. It stains deeply with Heidenhain's haematoxylin and after treatment with Mallory's stain appears bright brown in distinction to the endocuticula, which appears blue after the latter stain. Under the epicuticular layer of the terminal cap lies a thicker chitinoid layer the structure of which after the above treatment appears as delicately spongy. I interpret this

as the homologue of the "polster" or cushion of Sihler, 1924. The lateral limits of the terminal cap are well defined, and a space exists between it and

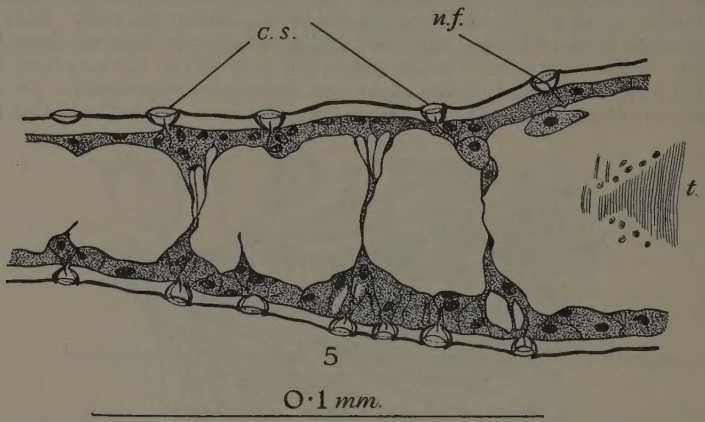

Fig. 5.—Transverse section across a gill. *c.s*, campaniform sensillae; *n.f*, nerve fibril; *t*, trachea.

the sides of the sensillary cup in which the major part of the organ is lodged. The under surface of the terminal cap, *i.e.* of the "polster," is slightly concave and to it are applied the cellular elements of the sensilla. These in all pre-

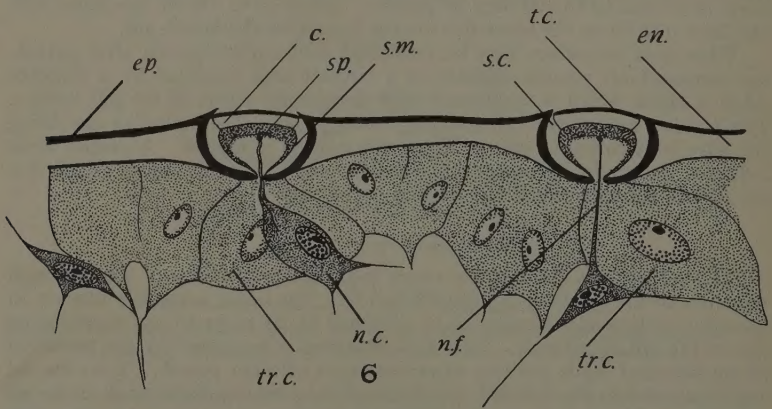

Fig. 6.—Composite diagram of a vertical section through two campaniform sensillae. *c*, cushion to the terminal cap; *en*, endocuticula; *ep*, epicuticula; *n.c*, nerve cell; *n.f*, nerve fibril; *s.c*, sensillary cup; *s.m*, supporting membrane; *sp*, scolopale; *t.c*, terminal cap; *tr.c*, trichogen cell.

parations are seen to perforate the basal pore of the sensillary cup and within the latter are confined so as to leave a space between the inner wall of the sensillary cup and themselves (fig. 6).

It has been possible with considerable difficulty to demonstrate a chitinous membrane covering these elements laterally and separating them from the lateral space within the sensillary cup. The regular occurrence of this peripheral space within the sensillary cup infers the existence of a limiting membrane to the cellular elements in those cases where the membrane itself has not been demonstrated with satisfactory clarity. The presence of the membrane here mentioned, and which serves as a support to the terminal cap, is also proved by the fact that in certain preparations through some accident of fixation or of cutting the whole of the sensilla has become dislodged from its cup but still remains attached to the gill by the nerve fibril. In such cases the cone shape of the sensilla is completely retained with its broad base still attached to the lower surface of the terminal cap, and from its inner apex can still be seen the emerging nerve fibril.

The protoplasmic parts so bounded by this supporting membrane are characterised by a conical form, the base of which is applied to the under surface of the " polster " of the cap, its apex pointing inwards and lying in the basal pore of the sensilla. Within this cone the cytoplasm is vacuolated, there being a marked concentration of cytoplasm beneath the polster and to a less extent along the sides of the cone (fig. 6). Across the vacuolated protoplasm there runs a nerve fibril from the sense cell situated in or below the hypodermis. This fibril terminates in a minute swelling under the centre of the " polster." The swelling stains deeply, and clearly lies in the cytoplasm and not in the substance of the terminal cap. It has been described in various terms by authors, *e.g.* " scolopale " by Newton 1931, " endknopfchen " by Sihler 1924, " sinneskorper " by Weber 1933. Passing inwards beyond the basal pore to the hypodermis we meet a single trichogen cell somewhat larger than normal hypodermal cells. It is the outer end of this cell which passes into the conical sensilla, and the cell as a whole presumably accounts for the formation of the terminal cap, its support-membrane and the scolopale. The trichogen cell calls for no further comment. The sense cell is stellate and can be traced from the scolopale inwards along the nerve fibril, with which it is continuous. In addition to the sensilla nerve it gives off other branches as the finest of fibrils into the body of the gill and along the inner surface of the hypodermis. Occasionally the sense cell lies athwart the trichogen cell, but more often is placed along the inner surface of the latter, over which its branches extend (fig. 6).

The description given here confirms in principle those given by Snodgrass 1926, Sihler 1924, Weber 1933 and Newton 1931. In *Locusta*, *Mantis* and in *Periplaneta* Sihler describes the scolopale as lying embedded in the polster of the terminal cap. Newton found the same condition to apply in *Apis*. This appears not to be the case in *Caenis*, a point of difference of no great importance. Sihler was able to detect considerable differentiation in the nerve fibril immediately behind the scolopale. In addition to the axial fibre to the nerve fibril, which can be seen only in rare cases in *Caenis*, he describes peripheral rib-like thickenings on the sides of the nerve fibre. Here again these have been seen so rarely and with so little distinction that I have not thought it advisable to refer to them specifically. In the cases of *Apis* and of the abovementioned Orthoptera described by Newton and by Sihler respectively, the sensillae are not embedded in cup-like depressions as in *Caenis*. The condition here described is more like that figured by Pflugstaedt 1912 in the sensillae of the halteres of Diptera, where the sensilla is shown as possessing a thick terminal cap supported on a fine chitinous membrane which is attached

to the wall of the sensillary cup at the sides of the basal pore. With Sihler 1924 as with Newton 1931 I am in entire agreement as to the non-perforate nature of the terminal cap, and thus do not support the findings of McIndoo 1914 in this respect.

Trichoid sensillae.

The trichoid sensilla is accommodated in a spherical depression lined by exocuticula as is the case with the campaniform type (fig. 7). The surface aperture through which the seta projects is narrow owing to the inward projecting edges of the cuticular cup. At the base of this cup, which is perforated for the passage of the nerve fibre, is found the supporting membrane to the seta. This is a delicate structure passing, as does the corresponding structure in the campaniform sensilla, from the base of the seta to the sides of the seta cup

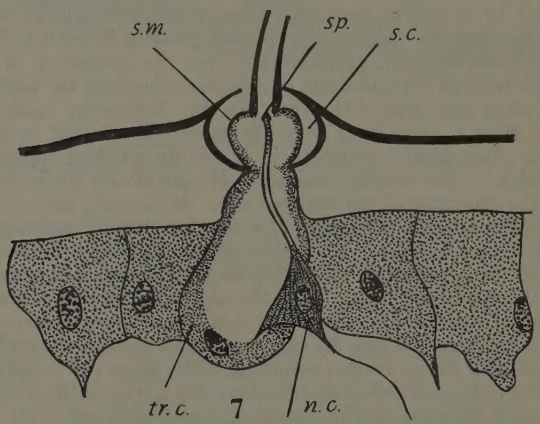

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Fig. 7.—Vertical section through a trichoid sensilla of a gill (semidiagrammatic). *s.m*, supporting membrane; *s.c*, sensillary cup; *sp*, scolopale; *tr.c*, trichogen cell; *n.c*, nerve cell.

near the place where the nerve fibre passes from the sense cell to the sensilla. Thus the trichoid sensilla is supported in a deep depression of the chitin by a membrane projecting from the bottom of that depression. The seta is hollow and presumably its fluid contents are in communication with the cytoplasmic structures found lower in the sensilla and around the nerve fibre. Where the seta is articulated to its supporting membrane is a minute scolopale lying at the end of the central axis of the nerve fibre, which reaches this point from the sense cell in the hypodermis. Such cytoplasm as lies in this confined region appears to be highly vacuolated, and is traceable to a large vacuolated cell in the hypodermis and across which lies a smaller stellate sense cell. The description given here calls for no further comment and agrees in principle with those given by Weber 1933, Sihler 1924 and Imms 1931 and 1935.

The above account refers to the sensillae both campaniform and trichoid which occur on the oscillating gills. In the case of such sensillae on the pseudo-elytra, the only significant difference lies in the depth of the endocuticula through which the nerve fibre and the trichogen cell have to pass from the

hypodermis to the sense organ. In the pseudo-elytral campaniform sensilla, the endocuticula tends to be excavated into a hemispherical space to accommodate the outer parts of the sense and trichogen cell. For the pseudo-elytral trichoid sensilla the endocuticula is perforated by the narrowest of canals, and one must assume in the absence of precise evidence that this canal contains both sense cell and trichogen cell elements. Plumose sensillae found sparsely scattered on the pseudo-elytral surface, resemble, with the exception of their fringed free borders, the trichoid variety. They are similarly associated with an even narrower endocuticular canal in which it has been impossible to define sense and trichogen elements. The scolopale at the end of the nerve fibre is clearly present and lies immediately beneath the open base of the fringed seta, but below the endocuticula so small are the cells and so little are they differentiated from the ordinary hypodermal cells that it has

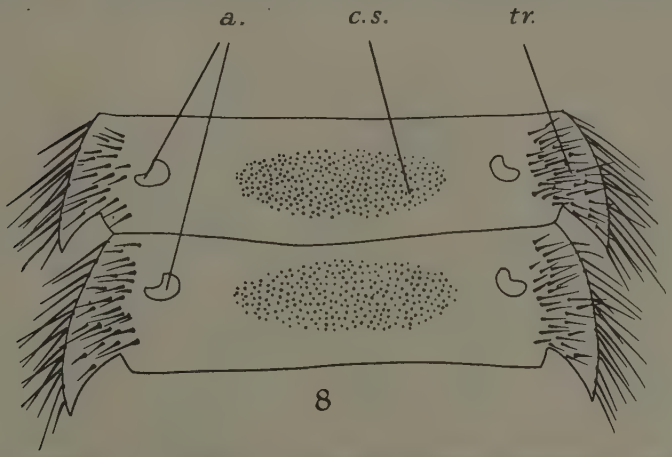

Fig. 8.—Surface view of the terga of two adjacent gill-bearing segments. *a*, articulation points for the gills; *c.s*, campaniform sensillae; *tr*, lateral fringe of trichoid sensillae.

not yet been possible to determine separate sense and trichogen elements. It may perhaps suffice that enough has been elucidated from their structure to establish that they are sense organs.

Sensillae on the gill-bearing segments.

It is not without interest to notice that campaniform sensillae such as those described above have only been found on three parts of the body of *Caenis*: (*a*) the gills, (*b*) the terga of gill-bearing segments and (*c*) on the upper surface of the basal plates of the labium. With the latter I do not propose to deal. The campaniform sensillae on the body segments which carry the gills are of interest in the present account in so far as they may be expected to be concerned with the same function as are the gill sensillae.

With the exception of the tergum of the seventh abdominal segment there are only campaniform sensillae on the terga of those segments which bear oscillating gills. On each of these segments the campaniform sensillae occupy an elliptical area across the middle between the points of gill articulation leaving a peripheral area free of them (fig. 8). The tergum of the third segment

bears about 160 sensillae, that of each of the succeeding segments, approximately 240, 300, 60 and 40 respectively. Thus only those regions over which water passes as a result of gill oscillation possess these structures, for although the seventh tergum is not gill-bearing it is overhung by the gills in front of it.

The whole of the gill region falling within the scope under consideration is also remarkable in that it is bounded on the two sides and at the back by setae. Each segment possesses along its lateral borders fringes of strong sensory setae which project outwards. In addition to these there are numerous other trichoid sensillae on the most lateral parts of the terga of the gill-bearing segments. These project laterally and upwards, while others on the tergum of segment seven form a posterior fringe which projects upwards and backwards. From this it may be seen that the gill region is as it were guarded all round, from in front by the pseudo-elytra and from the sides and behind by trichoid sensillae which are so arranged that water entering the intergill spaces from either side pours through a setose fringe before reaching the gills themselves.

Sensillae in relation to habits.

The part which the sensillae on the gills and related parts may play in the life of the animal may now be discussed.

If one examines the environmental waters from which the nymphs of this genus have been taken it is found to be of that clear kind which characterises the Cambridge Fens. Such water whether stagnant or slowly flowing is associated with a silty substratum, rich in organic matter and micro-organisms, the natural food of these animals. Though *Caenis* can often be taken clinging to water weeds or swimming freely in the water or even clinging by its claws to the surface film, it is found commonly to adopt a semi-burrowing habit. The silt in the bed of these waters is very easily disturbed, and thus forms at one and the same time a medium into which *Caenis* can easily burrow and one which it is easy to disperse into suspension. It has been observed that the animal crawls in a newt-like way with body close to the substratum and with legs outstretched. When doing this on the silt surface it gradually sinks therein, maintaining the horizontal attitude, until only its antennae, gills and cerci are raised above the level of the mud. It is then that the pseudo-elytra are raised and the underlying four pairs of gills oscillate, so producing a water flow over them from one side to the other. Under the quiet conditions which may prevail for considerable periods of time the water so passing over the gills is comparatively free from suspended particles.

So easily, however, is the mud disturbed by the creatures inhabiting this environment that a rapid change from clear to muddy water is effected. The particles in suspension tend to cling to the gills, particularly between their fringing filaments, and may be assumed to decrease their efficiency as organs of respiration. When such disturbances occur the pseudo-elytra are lowered over the now stationary gills and while still in this closed attitude the gills are slid from side to side under the depressed pseudo-elytra and so combed free of any entangling particles. It is, of course, impossible to see what is happening under the opaque pseudo-elytra in these movements, but it is quite clear that the gill fringes are drawn through those setae described above as forming a lateral guard to the gill area. In addition, it may be mentioned that the setae which project upwards and outwards from the lateral portions of the terga are likely to serve as a screen keeping the water passing through the gill area fairly free of those finer suspensions which lie in the water in

periods of relative quiet. It is also highly probable that the bands of comb-like microtrichia on the underside of the pseudo-elytra assist in combing the gills free of attached matter. In support of these considerations it should be mentioned that the general body surface of *Caenis* is always covered with much attached matter, including protozoa, diatoms and organic matter, and the only parts of the body which are relatively clean are the gills and the body surface over which the gills play.

That the pseudo-elytra are protective devices is beyond question, and that they preclude the antero-posterior water flow which characterises Mayfly nymphs not possessing them is equally obvious. Only nymphs of *Caenis* and of *Tricorythus* are known to possess such modified gills. These (*Tricorythus* has not been observed, but its anatomy is so like that of *Caenis* as to leave no doubts as to its behaving in a like manner) appear to be the only ones with a transverse flow, associated with a rhythm of gill movement peculiar to themselves, Eastham 1934. With the evolution of the pseudo-elytron it would appear that the normal rhythmical movements of the gills have undergone an accommodating change. It therefore appears to be an interesting case of a deep-seated thing like rhythm, being alterable to accommodate a structural change such as the one described, viz. the change of a gill to take on the part of a protective pseudo-elytron.

The phenomenon of current reversal, associated as already shown (Eastham 1934) with changes in direction of metachronal rhythm and in turning movements of the gills when in motion, may now be considered. It is the fact that, under experimental conditions of observation, reversal of flow can be induced by adding to the water passing over the gills, suspensions of fine particles in the water. Thus, for instance, if to an animal showing at a particular moment a flow from right to left, an additional suspension is added along the side of the body from which the water is passing, viz. the right side, the gills will cease working, the pseudo-elytra will close down momentarily, and often (though not in all observed cases) on the gills commencing to beat again they do so in such a manner as to throw the water in a direction opposite to that operating before, viz. from left to right.

Though this does not prove that the gill campaniform sensillae have anything to do in detecting differences in the thickness of suspensions in the water, nor preclude the possibility that the sensillae on the gills and neighbouring body surfaces have a chemotactic function, the inference may be drawn that they are mechanical sense organs, responding to the impact of particles in suspension and perhaps also in lesser degree to vibratory movements in the water.

Mention should be made of the possibly additional part played by these sensillae as stimulatory organs. The subject has been recently reviewed by Wolsky 1933, and it has been shown by a number of workers that in addition to specific receptor functions, sense organs may, by sending continuous impulses to the central nervous system, produce a condition of muscular tone essential for normal contraction. Among insects may be quoted the sensillae of the halteres of Diptera and the tibial organs of Locusts (Buddenbrock 1919 and 1930), the extirpation of which results in a loss of tone of the muscular system.

The removal of gills was not observed to produce any such results in the case of *Caenis*, though the retention of large numbers of campaniform sensillae on the terga of gill-bearing segments after such gill extirpation invalidates the suggestion that the gill sensillae are not stimulatory in function. In the

absence of precise experimental evidence no use can be served by pursuing this topic further here.

The sensillae in Caenis horaria.

The gills of this species were examined with a view to confirming the impression that gill sensillae, in the matter of their numbers and distribution, might afford a valuable systematic criterion for distinguishing the nymphs of different species from each other.

The pseudo-elytron of *C. horaria* is more quadrangular than in *C. macrura*, the sides being more parallel and the angles more abruptly rounded off. The campaniform sensillae on the lower side are confined more definitely to the middle region of the pseudo-elytron than in *C. macrura*. On the ventral side of the pseudo-elytron another prominent feature of difference is that while there is a band of fringed microtrichia running nearly parallel with the lateral border of the pseudo-elytron and extending from the latter's articulation point to its posterior border, this band is single and not multiple as in *C. macrura*. Thus at any one point along this band one only finds a single microtrichium with its free fringed edge pointing outwards towards the nearest point of the pseudo-elytral border. There are nearly 100 such microtrichia in this band.

Of the remaining gills, each, as in *C. macrura*, has both upper and lower surfaces divided into anterior and posterior areas by a band of trichoid sensillae, the posterior of which areas in each case is strongly pigmented and thereby shows up distinctly from the paler anterior area. The trichoid sensillae are definitely plumose (pl. 1), a feature which may be absent in *C. macrura* and when present in this species is not uniform for all the trichia. The numbers given below for the different kinds of sensillae on the gills of *C. horaria* are not to be regarded as constant. They represent an average from a number of counts and are sufficiently different from the numbers of sensillae found on *C. macrura* to be remarked upon. On the upper surface of the first gill about 60 plumose trichia form a band separating an anterior area with about ten from a posterior area with about six campaniform sensillae. On the lower surface a trichoid band of about 45 plumose sensillae separates anterior from posterior areas with as many as 70 campaniform sensillae in the latter but none in the former area. The upper surface of the second gill has a trichoid band of about 60 plumose setae. In front of this about 55 and behind it about 16 campaniform sensillae are to be found. About 45 plumose setae form the trichoid band on the lower side of this gill. There are about 40 campaniform sensillae behind this band but none in front of it. There are about 45 plumose trichia forming a band on the upperside of the third gill with about 40 campaniform sensillae in the area anterior to this and about 16 in the posterior area. On the third gill's lower surface the trichoid band consists of about 40 plumose setae and about 25 campaniform sensillae are found posterior to this band, and only in exceptional cases are a few such sensillae found anterior to it. On the fourth gill 36 plumose setae form a trichoid band on the upper surface. Only about 15 campaniform sensillae have been found in each area, anterior and posterior to this band. Twenty short plumose setae are found in the trichoid band on the lower surface of the fourth gill, with eleven campaniform sensillae behind this band but none in front of it. The terga of the gill-bearing segments resemble in the matter of sensillae those of *C. macrura* and call for no comment.

Summary.

The sensillae on the gills of *Caenis macrura* are described. On both pseudo-elytral and oscillating gills trichoid and campaniform sensillae are found. The pseudo-elytron possesses a fringe of trichoid sensillae, and on its lower surface many campaniform sensillae are present in the central area. Running from the point of articulation backwards and parallel with the outer border there is a band of fringed microtrichia, which probably serves as a comb by means of which the gills are kept free of mud and other particles in the water.

The oscillating gills possess each a band of trichoid sensillae running across both upper and lower surfaces. The campaniform sensillae found on both surfaces have a distribution which is described with reference to these trichoid bands.

The structure of the campaniform sensillae is described. One trichogen and one sense cell is present to each organ. The terminal cap of each is associated with a supporting membrane and with an underlying chitinoid cushion against which the scolopale at the end of the nerve fibril is applied. The trichoid sensillae are also described. Each possesses a single trichogen and a single sense cell. Similar sensillae to the above are found on the terga of gill-bearing segments.

The part which the sensillae may play in the life of the animal in relation to the environment is discussed, and it is suggested that the campaniform sensillae may serve to detect the bombardment by particles in suspension in the water. Their possible function as stimulatory organs for the maintenance of muscle tonus is not overlooked.

A brief comparison with *C. horaria* is made, and it is noted that the two species differ from each other in the number and distribution of their gill sensillae, the latter therefore forming an additional systematic criterion.

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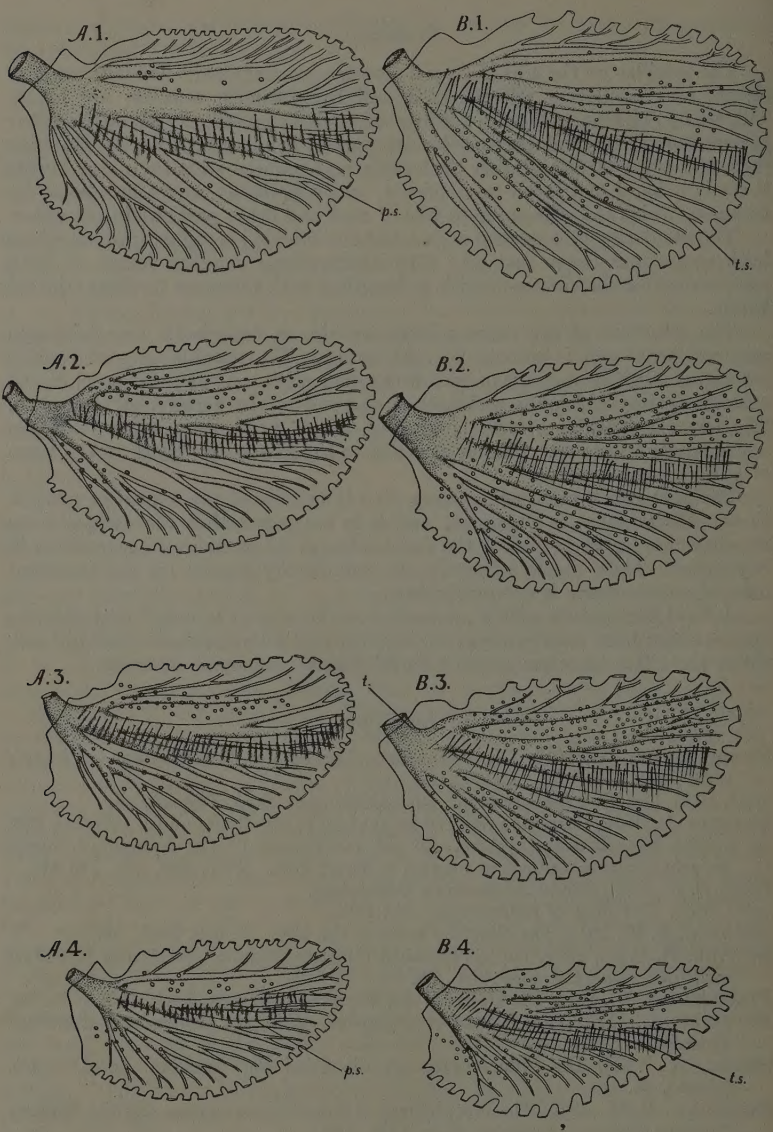

PLATE 1.

The dorsal surfaces of the four oscillating gills of the left side of *C. horaria* compared with the corresponding gills of *C. macrura*. A1–A4, *C. horaria*; B1–B4, *C. macrura*. *t*, trachea; *p.s*, plumose setae; *t.s*, trichoid setae; campaniform sensillae are indicated by small circles on all gills.